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HISTORICAL RECORDS OF CLIMATE-RELATED GROWTH IN *CASSIOPE TETRAGONA* FROM THE ARCTIC

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SUMMARY

(1) Shoots of the circumpolar species *Cassiope tetragona* were collected on brief visits to three remote arctic and subarctic sites, two in Svalbard and one in Swedish Lapland. The shoots were subsequently analysed by measuring leaf lengths in strict sequence along individual shoots.

(2) This evergreen species retained up to 232 leaves per shoot. Leaf lengths, plotted against leaf position on the shoots, revealed two trends: (i) more or less regular waves caused by the alternation of short spring and autumn leaves with long summer leaves, and (ii) an ontogenetic trend represented by a general increase in leaf length with increasing distance between the point of origin of the leaf and the origin of the shoot.

(3) The seasonal trend of leaf length was used to delimit annual complements of leaves, of which up to twenty persisted. The number of leaves was counted for each year and the ontogenetic trend of leaf length was removed by statistical methods so that leaf length indices could be calculated and relative lengths compared, both between years within populations and between populations. Three indices of leaf length were derived: maximum, minimum and the total of all leaf length indices for each year.

(4) Correlation analysis between the four measures of annual leaf performance showed several similarities between the two Svalbard populations, a few between the low altitude population from Svalbard and that from Swedish Lapland and none between the higher altitude Svalbard population and that from Swedish Lapland.

(5) Correlation analysis between annual leaf performance and mean monthly temperature and monthly total precipitation showed that July temperatures and precipitation during May were particularly important for leaf development in the Svalbard populations. July temperatures represent mid-summer conditions during a very short growing season in Svalbard, whereas May is normally the driest month in this region of generally low precipitation. Ambient temperature is usually sub-zero for most of May and precipitation as snow is probably important in protecting the sensitive shoot apices of *C. tetragona* which lack true buds.

(6) In Swedish Lapland, the number of leaves per year was correlated with summer temperatures but only negatively with precipitation which was greater at the Swedish site than in Svalbard. At the Swedish site, therefore, the protection of leaf primordia from frost is probably greater than in Svalbard because of a more persistent snow cover.

(7) Correlations between the number of leaves per year and leaf length indices in the previous year, together with correlations between leaf performance and weather conditions in the previous year, were often significant. In general, the same weather variables were correlated with leaf performance as in the within-year comparisons.

(8) The correlations between the number of leaves per year and the other measures of leaf performance and weather in the previous year were particularly strong in the Svalbard populations. This demonstrates the preformation of an annual leaf complement by the High Arctic Svalbard populations. This may be an important mechanism to buffer

production against particularly adverse weather conditions during the growing season. Leaf preformation was apparent but not so clearly demonstrated at the subarctic–alpine Swedish site.

(9) Significant multiple regression models of leaf performance were obtained in ten out of the twelve cases. Five models accounted for more than 50% of the variation in leaf performance and two of these accounted for more than 65%. The most significant relationships were found for total leaf length index at the two Svalbard sites and number of leaves per year at the Swedish site. Weather variables in the preceding year, particularly precipitation in May, were usually represented in the models.

(10) Retrospective analysis of the historical records of growth preserved in ungrazed herbaceous material from the Arctic can lead to the dating of specific events and the construction of models of long-term climate-related growth even though the period spent in the field is brief.

INTRODUCTION

Retrospective analyses of the past growth of long-lived plants and their populations provide a tool for understanding the relationships between plant performance and environmental factors such as weather. The retrospective approach obviates the need for prolonged observation during the current growth of the plants and their populations, and relies, instead, on the determination of the date and age of discrete growth increments. Dendrochronology, for example, has been used to describe relationships between tree growth and climate for periods extending back up to 8200 years (Fritts 1976). Over much shorter periods, but also long in observational terms, retrospective analyses of non-woody clonal plant populations have provided up to twenty-year records of plant module and population growth in graminoids and cryptogams (Callaghan 1988).

In some areas, such as the Arctic, dendrochronology is impractical because there are no trees, and dwarf shrubs have extremely small annual rings (0·07 mm–0·7 mm, Warren-Wilson 1964; Callaghan 1973) which may not be formed in some years. However, a knowledge of the relationship between the growth of plants and their populations and climate is important in this area for many reasons. In particular, climate change has been predicted to be greatest in polar regions (an increase in mean summer temperatures of 5 °C before the end of the Twenty-first century on Svalbard, for example; van Huis & Ketner 1987) and significant changes in plant growth and vegetation composition would be expected. Also, data on plant production in many arctic habitats, including polar semi-deserts, are required for investigating the causal relationships between fluctuations in climate and the performance of grazing animals such as reindeer (Tyler 1987).

Consequently, the selection and analysis of phytometers which are amenable to retrospective analysis, and which possess long historical records of growth, is an important substitute for dendrochronology. In northern latitudes, many species are amenable to retrospective growth analysis because (i) clear innate markers of annual growth are often identifiable in the plants' morphology due to the marked seasonality in growth caused by prolonged winter dormancy, (ii) decomposition rates are often slow and records of past growth may remain for many years, and (iii) modular clonal growth is common and large networks of interconnected modules are formed; interrelationships between modules which aid age determination can, therefore, be examined (Callaghan & Collins 1976).

This paper presents a retrospective analysis of the growth of the evergreen ericaceous dwarf shrub *Cassiope tetragona* in relation to weather conditions at two contrasting High Arctic sites in Svalbard, and at a subarctic–alpine site in Swedish Lapland.

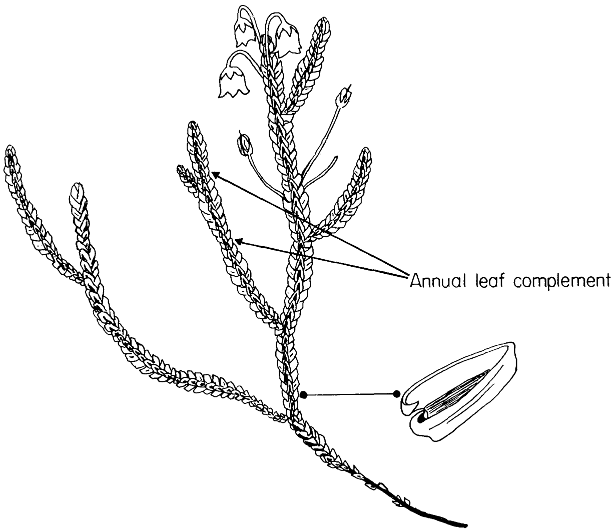

FIG. 1. Part of a shoot system of *Cassiope tetragona* showing the wave-like formations of leaves.

MATERIALS AND METHODS

Cassiope tetragona

Cassiope tetragona (L.) D. Don (Ericaceae) is an evergreen and xeromorphic dwarf shrub with solitary white pendulous bell flowers and imbricate scale-like leaves which are deeply grooved and occur in opposite pairs forming four rows (Fig. 1). The species is circumpolar (Hultén 1971) and reaches the highest latitudes (Böcher, Holmen & Jakobsen 1968). It is moderately chionophilic (Du Rietz 1942), and occurs on dry heaths and fell-fields, but is often found associated with the shelter of rocks or slopes where snow lies late (Polunin 1959). It apparently possesses secondary metabolites for defence and is not grazed.

The evergreen leaves of this species are particularly persistent and up to 232 leaves have been recorded on individual shoots representing the total leaf production for about twenty years. Leaves can remain green and therefore, presumably, photosynthetic for at least four years (Sørensen 1941). After three or four photosynthetic years the leaves change colour to yellow or red, and after one or two further years they apparently die and turn brown. Each row of leaves has a wave-like appearance due to a marked pattern of leaf-lengths associated with small leaves produced in autumn and spring alternating with larger leaves which expand in summer (Warming 1908). This offers the possibility of identifying the complements of leaves expanded in individual years and assessing the ages of shoots (Callaghan 1973) and the years of flowering, etc. It also enables the length and number of leaves produced in a particular year to be related to weather variables.

Study sites

Two High Arctic study sites were located in Adventdalen (78°15′N, 16°30′E), a broad valley on the west coast of Spitsbergen, the largest island in Svalbard. One site, the 'winter grazing site', was situated on a south-facing hillside at 200–250 m a.s.l. and was close to raised snow-free areas of semi-desert grazed by reindeer mainly in winter. *Salix polaris* Wg,

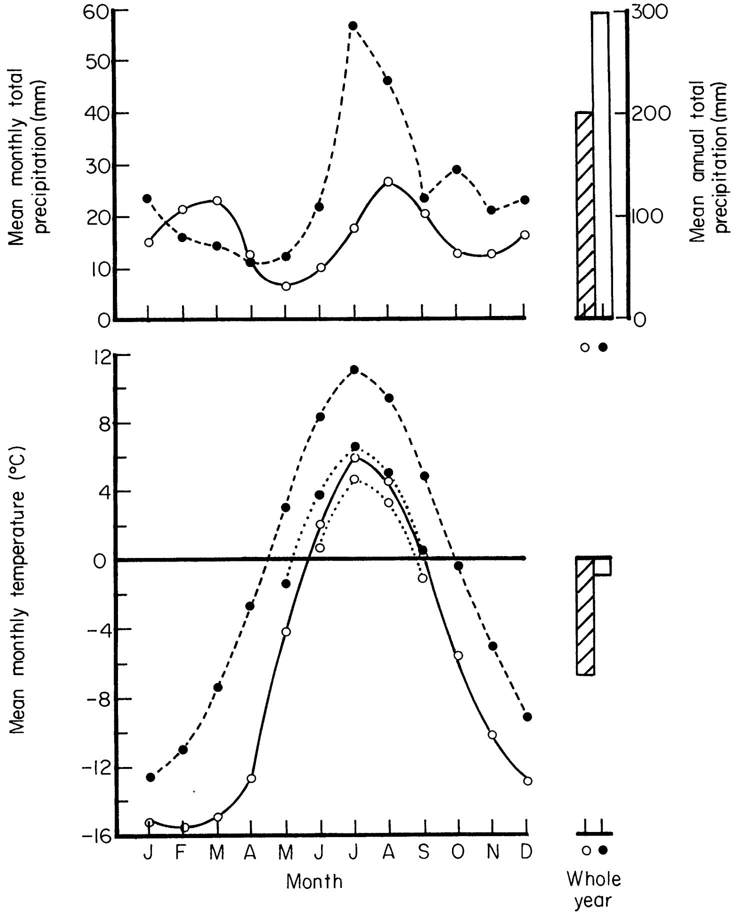

FIG. 2. A comparison of climate for the years 1967–86 inclusive between the Svalbard (○) and Swedish Lapland (●) sites (see text for sources). Dotted line signifies summer temperatures corrected for the altitude of the Swedish and Svalbard winter grazing sites using a lapse rate of 0·6 °C per 100 m. The lapse rate was not applied to the low-altitude summer grazing site.

Huperzia selago (L.) Bernh., *Polygonum viviparum* L., and *Carex rupestris* All. also occurred here. The second site, the 'summer grazing site', was located on the valley floor at an altitude of 25–50 m in an area dominated by *Dryas octopetala* L. and *S. polaris*. This site was grazed by reindeer in summer. A third site was established near the summit of Mount Slåttatjåkka in Swedish Lapland (68°22′N, 18°41′E) at an altitude of 1150 m in an area sparsely vegetated and grazed by reindeer in summer. Associated species were *C. bigelowii* Torr. ex Schwein., *Empetrum hermaphroditum* Hagerup., *Salix herbacea* L. and *S. polaris*.

Climate summaries of the general areas are presented in Fig. 2. In Svalbard, weather was recorded at Longyearbyen (37 m a.s.l.; 1967–1975) and Svalbard Lufthavn (28 m a.s.l.; 1976–1986) 12 km and 22 km from the winter and summer grazing sites, respectively. Temperature and precipitation data for Longyearbyen were amended by subtracting the difference between mean monthly values between the two meteorological stations in 1976 from earlier years (Steffensen 1982). In Sweden, climate data were provided by the Abisko Scientific Research Station at 380 m a.s.l. and some 5 km from the field site. Temperatures were corrected for the altitudes of the sites using a lapse rate of 0·6 °C per 100 m (Fig. 2).

Summer temperatures at Abisko are higher, and the growing season longer than in Svalbard and precipitation is also higher (Fig. 2). However, when the temperatures are corrected for altitude, the Slåttatjåkka site in Sweden appears very similar to the summer grazing site in Svalbard. The winter grazing site in Svalbard experiences the most extreme conditions of all three sites. Precipitation in Svalbard has a bimodal distribution and is generally low, particularly from spring to mid-summer (Fig. 2). Corrections of precipitation for particular sites were not possible although precipitation on Slåttatjåkka is likely to be much greater than at the weather station in Abisko (B. Å. Carlsson unpublished data).

Morphological analyses

Dominant shoots were selected at random from all three sites in July 1987 and were stored at −20 °C before being analysed. In the laboratory, two alternate rows of leaves were carefully removed in strict sequence from the apex to the base of the shoot and the maximum length of each leaf was measured to 0·1 mm. Leaf colour and axillary flowers and branches were recorded. Both alternate rows of leaves were analysed in a subsample of twenty plants from the winter grazing site only. Altogether, about 7800 leaves were measured from 136 sequences from all three sites.

Statistical analyses

Leaf length was plotted against leaf position for each sequence. Two trends of leaf length became evident. Firstly, a wave-like appearance described by Warming (1908) and Sørensen (1941) was evident due to the alternation of large summer leaves separated by small spring and autumn leaves. The number of leaves per year was, therefore, counted as the number of leaves occurring between two depressions in leaf length, assuming each year starts with the smallest leaf and that where the two smallest leaves are the same length, both belong to the current year (Fig. 3).

A second developmental trend also became evident, in which small leaves were produced in the first years of growth of a shoot (Fig. 3). This trend may be exaggerated to some extent by the shrinkage of senescing and dead leaves. In order to make between-years comparisons of plant performance (see below), it was necessary to remove this trend. Quadratic regressions of leaf length against leaf position were applied to each leaf sequence. Data for the current year (1987) were omitted because leaf expansion could still occur. The first point in the regression was that for the peak of the earliest year (see start and end points of the regression line in Fig. 3). Weighted deviations of leaf length were then calculated in a method analogous to that used in studies of dendrochronology (Fritts 1976), i.e.

$$\mathrm{wd} = (\mathrm{ol} - \mathrm{el})/\mathrm{el}$$

where wd = weighted deviation in leaf length or leaf-length index, ol = observed leaf length and el = expected leaf length interpolated from the regression equation. After these calculations, the following measures of annual performance were extracted (see also Fig. 3): (a) the total of all leaf-length indices for each year, (b) the maximum leaf-length index for each year and (c) the minimum leaf-length index for each year.

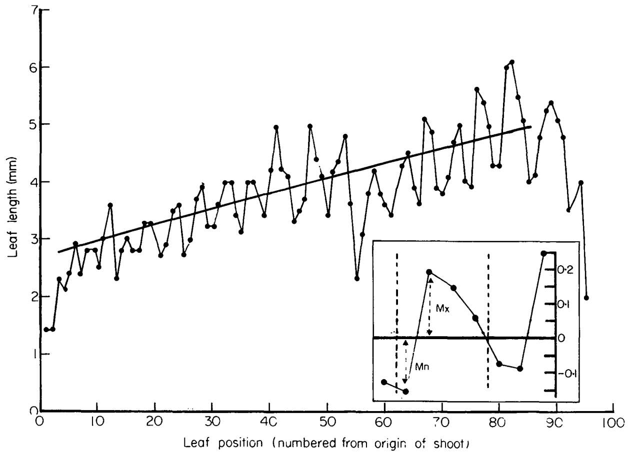

FIG. 3. Example of variations in leaf lengths related to position in *Cassiope tetragona*. The thick line represents the regression: leaf length = a + b × position − c × position^2. The bottom inset shows the way in which the deviations of leaf length were converted into length indices for one year (limits denoted by vertical broken lines). The following assessments of leaf performance were extracted: (i) Number of leaves per year (number of leaves between the vertical broken lines). (ii) Maximum leaf-length index (Mx) calculated as the maximum of: (observed − expected leaf length)/expected leaf length, where expected leaf length is interpolated from the regression (thick horizontal line). (iii) Minimum leaf index (Mn) calculated as above. (iv) Total leaf-length index, which is the sum of all leaf-length indices of the year.

The replicates of these parameters, together with the number of leaves per year, were correlated with each other within each population. However, all other correlations were based on means weighted for different sample sizes. Correlations with weather variables were restricted to those for the summer months in which mean temperatures exceeded 0 °C (Fig. 2). Weather variables which were significantly correlated with a leaf performance parameter were included in a step-wise linear multiple regression model. The regressions were based on means weighted for different sample sizes and a significance level of 0·15 was used for the retention of weather variables.

RESULTS

Leaf performance

The number of leaves per year varied greatly from year to year at each site with a range of four to twenty-four leaves per year. Over all of the years investigated, it was surprisingly similar between populations from all three sites, but there was a significantly lower value at the Svalbard winter grazing site (Table 1). Absolute leaf length was significantly different between all sites and was greatest at the Svalbard summer grazing site and lowest at the Swedish site (Table 1).

When the seasonal and ontogenic trends of leaf length are removed, it is possible to compare leaf-length indices for particular years between populations. Total and minimum leaf-length indices are signficantly correlated between the populations from the two Svalbard sites (Table 2). However, there are no significant correlations between any of the leaf-length indices measured in the Svalbard winter grazing and Swedish Lapland

TABLE 1. Between-site comparison of leaf performance parameters in *Cassiope tetragona.*

	Svalbard winter grazing	Svalbard summer grazing	Swedish Lapland
Mean number of leaves per year ± S.E.	10·25 ± 0·084	12·62* ± 0·196	12·23* ± 0·180
Range	4–16	6–24	4–24
Mean leaf length (mm) ± S.E.	3·95 ± 0·013	4·48 ± 0·015	3·85 ± 0·015
Range	1·3–6·8	2·0–7·4	1·6–6·4
Number of leaves sampled	3298	2074	2447
Number of annual leaf complements sampled	710	301	400
Number of leaf sequences sampled	57	41	38

*These means were not significantly different.

populations. In contrast, the number of leaves per year and minimum leaf-length index are significantly correlated between the Swedish and Svalbard summer grazing populations (Table 2). Thus, parameters of leaf performance have fluctuated between years in a similar way in the populations at the two Svalbard sites, but there are fewer similarities between the Svalbard summer grazing population and the Swedish population, and no similarity between the Svalbard winter grazing population and the Swedish population.

In the Svalbard winter grazing population, a comparison of the four parameters of leaf performance shows that they are all significantly correlated with each other in the same year (Table 2). Interestingly, however, the number of leaves per year is highly significantly correlated with total and minimum leaf-length indices in the previous year (Table 3).

In the Svalbard summer grazing population, all four parameters of leaf performance are again significantly inter-correlated (Table 2). Once again, the annual number of leaves is significantly correlated with the total leaf-length index in the previous year (Table 3). This effect can be clearly seen when data from the two populations are combined (Fig. 4).

In the Swedish population, all four parameters of leaf performance are significantly inter-correlated (Table 2) and the number of leaves per year is significantly correlated with the three-leaf length indices in the previous year (Table 3).

There are only three correlations which reach significance at the 5% level between leaf-length indices in the current and previous years (Table 3). Two of these are at the Svalbard winter grazing site.

Leaf performance and weather conditions

In general, the variations in total leaf-length index and the number of leaves per year for the two Svalbard populations combined suggest periods of adverse weather in 1968, 1973–74, 1976 and 1981–84 (Fig. 4). These periods alternate with apparently favourable weather conditions in the years 1969–72, 1975, 1978–79 and 1985–86 (Fig. 4).

Correlation analysis revealed several significant associations between leaf performance and weather variables involving lag periods of one year or more. Fewer significant correlations existed between leaf performance parameters and weather conditions during

TABLE 2. Correlation coefficients and sample sizes (in parentheses) of annual leaf performance parameters in *Cassiope tetragona* based on individual replicates (correlations between leaf performance parameters within populations) and on means weighted for different sample sizes (between population correlations for each leaf performance parameter). LN = number of leaves year^{-1}; TLLI = total leaf-length index year^{-1}; MXLLI = maximum leaf-length index year^{-1}; MNLLI = minimum leaf-length index year^{-1}.

		Svalbard winter grazing				Svalbard summer grazing				Swedish Lapland			
		LN	TLLI	MXLLI	MNLLI	LN	TLLI	MXLLI	MNLLI	LN	TLLI	MXLLI	MNLLI
Svalbard winter grazing	LN				(710)								
	TLLI	0·17***											
	MXLLI	0·39***	0·77***										
	MNLLI	−0·16***	0·52***	0·12**									
Svalbard summer grazing	LN	0·44 N.S.			(14)				(301)				
	TLLI		0·78***			0·21***							
	MXLLI			0·27 N.S.		0·29***	0·54***						
	MNLLI				0·66*	0·04*	0·49***	0·14*					
Swedish Lapland, Slåttatjåkka	LN	0·46 N.S.			(17)	0·56*			(14)				(400)
	TLLI		0·41 N.S.				0·53 N.S.			0·18***			
	MXLLI			0·18 N.S.				0·14 N.S.		−0·11*	0·51***		
	MNLLI				0·45 N.S.				0·54*	0·42***	0·78***	0·17***	

* $P<0{\cdot}05$; ** $P<0{\cdot}01$; *** $P<0{\cdot}001$; N.S., $P>0{\cdot}05$.

TABLE 3. Within-population correlation analyses of annual leaf performance parameters in *Cassiope tetragona* based on means weighted for different sample sizes comparing the number of leaves per year in the current year (year C) with leaf-length indices in the previous year (year C − 1). Each leaf-length index is also correlated with its value in the previous year. Correlation coefficients and sample sizes (in parentheses) are presented. LN = number of leaves year^{-1}; TLLI = total leaf-length index year^{-1}; MXLLI = maximum leaf-length index year^{-1}; MNLLI = minimum leaf-length index year^{-1}.

		Year C			
	Year C − 1	LN	TLLI	MXLLI	MNLLI
Svalbard winter grazing	LN	0·19 N.S.			(19)
	TLLI	0·64**	0·55*		
	MXLLI	0·44 N.S.	—	0·41 N.S.	
	MNLLI	0·80***	—	—	0·54*
Svalbard summer grazing	LN	0·74**			(13)
	TLLI	0·58*	0·47 N.S.		
	MXLLI	0·38 N.S.	—	0·21 N.S.	
	MNLLI	0·50 N.S.	—	—	0·35 N.S.
Swedish Lapland, Slåttatjåkka	LN	0·35 N.S.			(16)
	TLLI	0·74**	0·47 N.S.		
	MXLLI	0·69**	—	0·16 N.S.	
	MNLLI	0·83***	—	—	0·51*

* $P<0{\cdot}05$; ** $P<0{\cdot}01$; *** $P<0{\cdot}001$; N.S. $P>0{\cdot}05$.

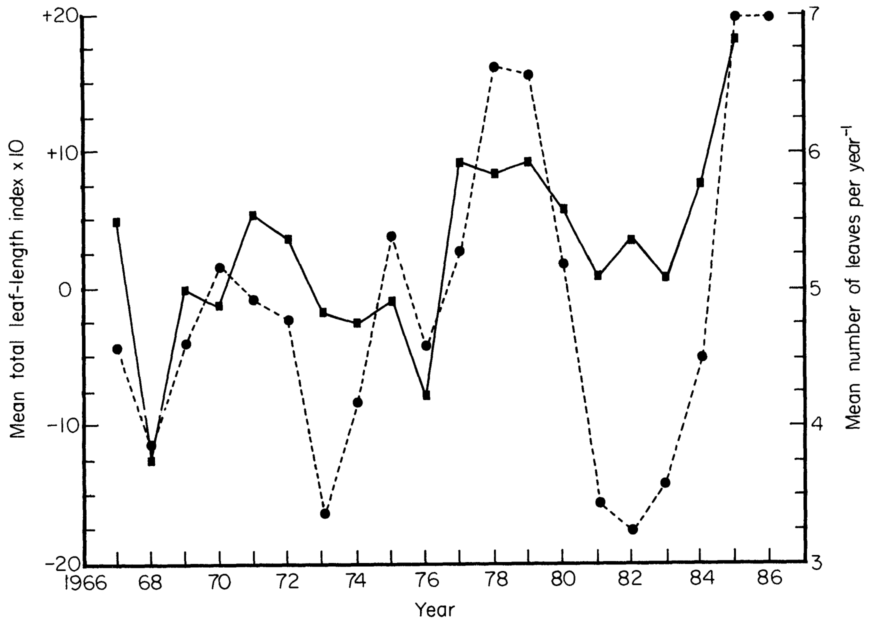

FIG. 4. Correlation between the number of leaves produced year^{-1} by *Cassiope tetragona* (– – –) and the total leaf-length index in the previous year (———). Data for the winter and summer grazing sites in Svalbard were combined.

TABLE 4. Correlation coefficients, based on means weighted for different sample sizes, between leaf performance and weather variables. Only correlations significant at the 5% level are included. C, weather variables for current year; C − 1, weather variables for previous year; T, monthly mean temperature; P, monthly total precipitation.

Site	Year	Number of leaves year^{-1}	Total length index	Maximum length index	Minimum length index
Svalbard, winter grazing ($n = 20$)	C	Sept P 0·48	July T 0·57	May P 0·65	July T 0·61
		.	.	June P −0·52	.
		.	.	Aug P −0·57	.
		.	.	Sept P −0·53	.
		.	.	July T −0·46	.
	C − 1	May P 0·52	May P 0·79	May P 0·45	May P 0·89
		July T 0·50	Aug P −0·63	June P −0·52	Aug P −0·45
		.	July T 0·77	May T 0·55	July T 0·55
		.	.	.	Aug T 0·47
Svalbard, summer grazing ($n = 14$)	C	.	May P 0·56	June T 0·70	May P 0·73
		.	July T 0·77	July T 0·66	July T 0·78
		.	.	.	Aug T 0·63
	C − 1	May P 0·66	May P 0·73	May P 0·64	May P 0·60
		July T 0·54	Aug P −0·63	Aug P −0·76	June P −0·57
		.	July T 0·69	July T 0·77	May T 0·63
		.	.	.	June T 0·65
Swedish Lapland Slåttatjåkka ($n = 17$)	C	July P −0·51	June T 0·64	.	June T 0·52
		Aug P −0·50	.	.	.
		June T 0·71	.	.	.
		July T 0·64	.	.	.
	C − 1	.	June P −0·66	June P −0·58	June P −0·68
		.	July T −0·51	.	July T −0·61
		.	Sept T −0·57	.	Sept T −0·59

the current year (Table 4). Overall, however, the correlations based on the longer lag periods tended to be random and less biologically meaningful than the correlations between leaf performance and weather in the current or previous year. Thus, in the current and previous year, temperatures in June (10% of the significant correlations), and particularly July (29%), together with precipitation in May (21%), June (12%) and August (12%) were the most important variables (Table 4).

When the correlations between individual leaf performance parameters and weather are examined (Table 4), it can be seen that the number of leaves per year is correlated with four weather variables in the current year at the Swedish site, compared with a maximum of one at the Svalbard sites. On the other hand, the number of leaves is not correlated with any weather variables in the previous year at Swedish site, but is correlated with July mean temperature and precipitation in May in the previous year at the two Svalbard sites. The maximum leaf-length index is correlated with weather during both the current and preceding years at the Svalbard sites, while there is only one significant correlation with a weather variable at the Swedish site. The minimum and total leaf-length indices are also correlated with weather variables in both the current and preceding years at all three sites (Table 4).

The trends of correlation between weather and parameters of growth are not as clear at the Swedish site as at the two Svalbard sites. However, summer temperatures, particularly in June, are significant, as would be expected, but precipitation is only negatively correlated with leaf growth (Table 4). At the Svalbard sites, positive correlations between leaf growth and spring and summer temperatures and spring precipitation are evident, together with negative correlations between leaf growth and summer precipitation (Table 4).

Multiple regression analysis

Regression analysis was restricted to considering weather variables in only the current year and preceding year because (i) correlations found with a lag of one year adequately demonstrate a general lag effect; (ii) there are indirect effects of weather on leaf development which involve resource acquisition by older leaves in previous years and subsequent resource availability to the growth of new leaves: this mechanism is of less interest here; (iii) weather conditions correlated with leaf growth in earlier years are less biologically meaningful than those in the current or preceding years, and occur at random.

Significant multiple regression models were obtained for ten of the twelve site × leaf parameter combinations. Two of the models accounted for 64% and 74% of the variation in leaf performance and a further three accounted for more than 50% of the variation (Table 5). The most significant regression models were obtained for the Svalbard winter grazing population. The leaf performance parameters best described by weather at each site were total leaf length index at the two Svalbard sites and number of leaves per year at the Swedish site. Only between 34% and 50% of the variation in number of leaves per year was explained at the three sites (Table 5).

The weather variables retained in the regression models mainly related to the preceding year and those relating to the current year were found in only three of the ten significant models. Precipitation was again important in explaining leaf performance and precipitation in May was particularly important, occurring in six of the ten significant models (Table 5). Mean monthly temperature was included in the models less often than precipitation, although July temperature occurred in three of the significant models.

DISCUSSION

It has been known since the turn of the century that *Cassiope tetragona* possessed leaves which varied in length and thereby marked the annual growth increments of the shoots (Warming 1908). However, no quantitative estimates of annual growth were made, although Warming (1908) states that between eight and twenty-four leaves were produced per year. Correlations with other variables were also lacking although Sørensen (1941) noted that flowers were only produced when more than six pairs of leaves were produced in a year.

The present study has developed these early observations by giving quantitative estimates of annual shoot growth, based on four different assessments of annual leaf performance, and by relating these to weather conditions over an historical period of up to twenty years. It has also formalized this information into predictive multiple regression models of leaf performance in terms of weather conditions at the three sites.

TABLE 5. Multiple regression models based on means weighted for different sample sizes for each of the *Cassiope tetragona* leaf performance variables at each of the sites. A significance level of 0·15 was used for the inclusion of weather variables. P, precipitation; T, temperature; LN = number of leaves year^{-1}; TLLI = total leaf-length index year^{-1}; MXLLI = maximum leaf-length index year^{-1}; MNLLI = minimum leaf-length index year^{-1}. All leaf-length indices were multiplied by 10 for convenience.

Site	Dependent variable		Model	*F* Ratio	r^2	S
Svalbard winter grazing	LN	=	4·59+(0·024 × Sept. P year C)+(0·086 × May P year C−1)	$4·7_{2,17}$	0·36	*
	TLLI	=	2·47+(0·53 × May P year C−1)−(0·069 × Aug. P year C−1) +(1·68 × July T year C−1)	$15·0_{3,16}$	0·74	***
	MXLLI	=	−7·94−(0·29 × June P year C)+(1·63 × May T year C−1)	$8·6_{2,17}$	0·50	**
	MNLLI	=	−11·38+(2·46 × May P year C−1)−(0·17 × Aug. P year C−1)	$17·0_{2,17}$	0·67	***
Svalbard summer grazing	LN	=	4·55+(0·17 × May P year C−1)	$6·1_{1,12}$	0·34	*
	TLLI	=	−17·49+(2·42 × May P year C−1)	$12·4_{1,12}$	0·51	**
	MXLLI	=	11·70+(0·58 × May P year C−1)	$5·3_{1,12}$	0·31	*
	MNLLI	=	−35·36+(2·94 × Aug. T year C)+(0·54 × May P year C−1)	$3·9_{2,11}$	0·41	N.S.
Swedish Lapland, Slåttatjåkka	LN	=	1·48−(0·013 × Aug. P year C)+(0·46 × July T year C)	$7·1_{2,14}$	0·50	**
	TLLI	=	0·34−(0·0018 × June P year C−1)−(0·014 × July T year C−1)	$5·3_{2,14}$	0·43	*
	MXLLI	=	No significant model			
	MNLLI	=	0·207−(0·0097 × June P year C−1)	$9·5_{1,15}$	0·39	**

* $P<0·05$; ** $P<0·01$; *** $P<0·001$; N.S., $P>0·05$.

The number of leaves per year and the maximum and minimum length indices should be largely independent, whereas total leaf-length index is determined both by the number of leaves and by their lengths.

Although there is considerable variation between years in the different measurements of leaf performance, the variations were consistent between sites, particularly between the two independent Svalbard sites. The numbers of leaves per year in the Svalbard populations were similar to the values determined by Warming (1908) for Greenland plants (eight to twenty-four) and Callaghan (1973) for plants from Devon Island (six to ten). Leaf length tended to vary more than number of leaves per year, with the largest leaves being found at the lowland summer grazing site. The leaves from all three sites in this study were generally larger than those found on Devon Island (range 2·0–4·5 mm, Callaghan 1973).

Correlation analysis showed that the four measurements of leaf performance were significantly correlated with each other at each site. Also, the number of leaves per year was significantly correlated with the total leaf length index in the preceding year.

The relationship between number of leaves per year and total leaf-length index in the preceding year is undoubtedly due to the preformation of at least one year's leaf complement. Indeed, some of these leaves can be seen in Fig. 3. The preformation of flower buds in arctic plants has been known for a long time (Resvoll 1917; Sørensen 1941; Hodgson 1966), and also occurs in *C. tetragona* (Sørensen 1941). However, although the apex of a shoot of *C. tetragona* was regarded as an over-wintering bud protected by small leaves rather than bud scales (Warming 1908; Sørensen 1941), the degree of leaf preformation was apparently not appreciated.

The dependence of the number of leaves in a particular year on the biomass of leaves in the preceding year, represented by total leaf-length index, acts as an important buffer against exceptionally severe growing seasons. In one favourable growing season following another, leaf biomass in the current year should be high due to a combination of a large number of leaves and large leaf lengths. If the next growing season is adverse, biomass will tend to be reduced because of the small size of the leaves but the complement of leaves will, nevertheless, be large due to its preformation in the previous favourable growing season. This will minimize the reduction in biomass. If a favourable growing season now follows, the leaf complement will be small but this will be compensated for by the increased length of the leaves. Thus, similar leaf biomass can be attained in different years by small numbers of large leaves or large numbers of small leaves, according to weather conditions. Such a mechanism which buffers annual variation in growth could be of considerable importance in the short growing seasons (two to three months) at these arctic sites, where small changes in the length of the growing season, or conditions in it, could otherwise have serious effects on growth, reproduction and survival. The preformation of leaves, together with the lack of a true bud, also aids fast leaf development when the snow cover recedes.

The relationships between weather and the four measures of leaf performance again emphasize leaf preformation and subsequent expansion, particularly at the Svalbard sites. The number of leaves per year is correlated with four weather variables in the preceding year compared with only one in the current year at the Svalbard sites. In contrast, the three measures of leaf length were correlated with almost as many weather variables in the current year as in the preceding year. Similarly, weather variables for the current year are included in only three of the ten significant regression models whereas weather variables in the preceding year are included in nine of the ten models. Based on the correlation analyses and multiple regression models, the weather conditions of particular importance are July temperatures and precipitation in May for the Svalbard sites. July is the warmest month in Svalbard and would, therefore, be expected to play a significant role in leaf formation and development. May, in contrast, is the driest month (6·4 mm). It would seem, therefore, that changes in precipitation during this month are critical to the development of leaves of *C. tetragona*, even though this species has xeromorphic features.

The mechanism of the control is probably related to prolonged snow cover in spring and protection of growing points rather than moisture for growth as the mean temperature in May is −4·1 °C. *Cassiope tetragona* is moderately chionophilic (Du Rietz 1942, Polunin 1959) and at the Svalbard sites it was often restricted to the base of slopes where snow lies longest. The absence of true bud scales would make such protection by late snow important.

It was evident that all of the thirteen significant correlations between leaf growth and precipitation for the months June to August were negative at all three sites. This could reflect poor growing conditions during summer associated with increased cloud cover and reduced light during periods of rain.

The effect of weather on leaf production and development was similar in both Svalbard populations, with a few exceptions. June temperature was highly significantly correlated with maximum length index at the summer grazing sites, perhaps indicating an earlier start of the growing season at this more favourable site.

In contrast, there were large differences in the relationships of leaf development and weather between the Swedish and Svalbard populations. In particular, the number of leaves per year in the Swedish population was controlled (i.e. there were highly significant correlations) mainly by summer temperatures in the current year, not in the year before. Precipitation, moreover, was relatively unimportant at the Swedish site according to the correlation analyses, while only negative correlations of questionable biological meaning were found in the preceding year. Preformation of leaves was, therefore, less well demonstrated at the climatically less extreme Slåttatjåkka site. The greater precipitation here is relatively unlimiting (i.e. all correlations between leaf performance and precipitation were negative), and *C. tetragona* is not so clearly associated with patches experiencing longer snow-lie at the Slåttatjåkka site.

When the relationships between leaf performance and weather are formalized by stepwise multiple regression analysis, it can be seen that over 67% of the variation was accounted for in two cases, and over 50% in a further three cases. This is surprising as the weather variables were measured some distance away from the sites and generally apply to whole regions, rather than to the specific microclimates of the individual sites. At each site, at least 50% of the variation in a leaf performance parameter can be accounted for by weather variables which are mainly precipitation at the two Svalbard sites. As the spring and early summer of 1988 have been particularly dry on Svalbard, it will be possible to predict leaf performance from the regression models and then validate this in future years. The use of four different assessments of growth in a retrospective analysis has, therefore, enabled much information to be obtained from a brief visit to remote field sites.

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